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Review article

Harmful algal blooms in inland waters

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Abstract

Harmful algal blooms can produce toxins that pose threats to aquatic ecosystems and human health. In this Review, we outline the global trends in harmful algal bloom occurrence and explore the drivers, future trajectories and potential mitigation strategies. Globally, harmful algal bloom occurrence has risen since the 1980s, including a 44% increase from the 2000s to 2010s, especially in Asia and Africa. Enhanced nutrient pollution owing to urbanization, wastewater discharge and agricultural expansion are key drivers of these increases. In contrast, changes have been less substantial in high-income regions such as North America, Europe and Oceania, where policies to mitigate nutrient pollution have stabilized bloom occurrences since the 1970s. However, since the 1990s, climate warming and legacy nutrient pollution have driven a resurgence in toxic algal blooms in some US and European lakes, highlighting the inherent challenges in mitigating harmful blooms in a warming climate. Indeed, advancing research on harmful algal bloom dynamics and projections largely depends on effectively using data from multiple sources to understand environmental interactions and enhance modelling techniques. Integrated monitoring networks across various spatiotemporal scales and data-sharing frameworks are essential for improving harmful algal bloom forecasting and mitigation.

Sections

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Introduction

Harmful algal blooms (HABs) are increasingly prevalent in inland waters and are a growing global environmental concern[1]. Algal blooms form in aquatic systems where light and nutrient levels, among other factors, are sufficiently high to favour rapid phytoplankton growth[2]. However, if the bloom-forming phytoplankton species release toxins or if excessive proliferation of algal biomass disrupts normal ecosystem functioning then blooms are considered to be harmful[3] (Table 1). Death and decomposition of HAB biomass leads to depletion of dissolved oxygen and hypoxia, which can create dead zones where fish and other aquatic organisms can no longer survive[4]. Toxin-releasing HAB species, including some cyanobacteria, can further exacerbate fish mortality (Fig. 1), while also posing a risk to human health. Thus, there is a pressing need to mitigate HABs and their negative impacts on aquatic ecosystems, human health and local economies[5].

Advances in satellite remote sensing[6] have enabled global-scale observations of inland waters and have revealed widespread increases in HAB occurrences since the 1970s. Nutrient availability, particularly of phosphorus and nitrogen, is a key factor controlling the occurrence and proliferation of HABs[7]. Widespread nutrient enrichment of inland waters since the 1960s, owing to nutrient pollution from human activities such as agricultural fertilizer use and urbanization, is considered a key factor driving the observed trends in HAB occurrence. In the 1970s, some high-income regions put policies in place to limit nutrient pollution yet have still experienced increasingly frequent HABs since the 1990s. Where nutrient discharge is restricted, blooms are instead driven by legacy effects of past nutrient pollution and the influence of global warming[8]. Rising temperatures driven by climate change are promoting HAB formation through enhancing water stratification, which helps surface algal scum to aggregate, and promote growth rates while also favouring toxin-producing cyanobacteria[9] over non-toxic species[10]. Indeed, harmful cyanobacterial blooms have now become a yearly phenomenon in numerous lakes worldwide in the warming climate[1].

Cyanobacterial blooms, often referred to as CyanoHABs, contaminate water bodies and water supplies, potentially leading to water crises and substantial economic losses. For example, annually in the United States, CyanoHABs render affected water bodies unsuitable for recreational activities, drinking water and agricultural use, resulting in annual losses of approximately 2 billion US dollars[11]. Similarly, algal contamination of Lake Taihu, China, in 2007 and Lake Erie, USA, in 2014 led to water crises where residents in nearby cities were left without safe drinking water[12,13]. Thus, mitigating HABs and managing their detrimental impacts are important aspects of achieving the United Nations' sustainable development goals (SDGs), in particular human health (SDG 3), water security (SDG 6) and biodiversity conservation (SDGs 14 and 15)[14]. However, achieving these goals requires an understanding of the global-scale spatiotemporal patterns of HABs, their underlying drivers and their future trajectories.

In this Review, we explore the global trends in HAB occurrence in inland waters and focus on identifying HAB hotspots. We discuss the factors that drive these trends and hotspot, and consider the future trajectory of HABs in a warming climate. Finally, we provide suggestions for integrated interdisciplinary monitoring of HABs and data sharing to help better inform HAB prediction and mitigation.

Temporal trends and geographical distribution

Since the 1970s, satellite remote sensing has aided long-term monitoring of HABs over broad spatial scales[6]. Advances in cloud computing have enabled reanalysis of remote-sensing data obtained since the 1980s and further extended the spatiotemporal coverage of observations to provide greater insights into global patterns in HAB occurrences[1,15,16]. The following sections discuss trends in global HAB hotspots, with a focus on lakes and reservoirs in regions experiencing severe HABs or widespread impacts.

Global trends

Satellite-derived observations between 1982 and 2019 indicate that HABs have occurred in 11.7% of the global lake area across all continents (Fig. 2a), equivalent to 8.8% of the 248,243 lakes larger than 0.1 km^2 (refs. 1,2). Most global-scale observations indicate an overall increase in HAB frequency since the 1970s, but there is variability in the strength and direction of trends over time and between regions[1,15,17] (Fig. 2b,c). Globally, between the 1980s and 2000s, HAB occurrences remained relatively stable, but in the 2010s there was a 44% increase in global bloom frequency, which was primarily driven by higher occurrences in Asia and Africa[1]. The majority of recorded bloom outbreaks have been in temperate lakes (35–65° N), including North America, Northern and Western Europe, and West and East Asia. Exposure to stressors such as human population growth, intensified agricultural production, industrialization and species invasions has led to 63% of lakes larger than 25 km^2 being classified as eutrophic[18,19]. Policies to reduce nutrient inputs to lakes have been successful in some regions, but their success in long-term HAB mitigation has been mixed (Fig. 3). This variation in the efficacy of HAB mitigation measures highlights the need to consider the heterogeneity of factors influencing HAB formation from local and regional scales.

Asia

There has been a substantial increase in HABs since the early 1980s in Asian lakes, particularly in China and India[1]. The increase in HABs is closely linked to rapid population growth and economic expansion, which have led to greater discharges of industrial and domestic wastewater, widespread use of agricultural fertilizers, and intensive aquaculture activities[20–22]. Lakes on the Yangtze Plain in China, such as Taihu and Chaohu[23], are particularly affected and experience frequent algal blooms[24,25]. Economic and demographic expansion has exacerbated nutrient loads[21,26], despite efforts to mitigate nutrient pollution, including hydraulic projects diverting water from the Yangtze River into Lake Taihu[27]. There has been a pronounced increase in HAB occurrences in Chinese lakes between 2003 and 2020 (Fig. 2d). Among the 103 bloom-affected lakes, 95 experienced an increased harmful bloom occurrence, 79 saw an earlier seasonal bloom onset, and 97 had prolonged bloom periods[20]. The Caspian Sea has experienced an increase in chlorophyll-*a* concentrations and cyanobacterial blooms between 2003 and 2017 due to elevated nutrient discharges from rivers[28–30]. Similarly, Lake Baikal in Russia has experienced regular HABs in shallow nearshore zones since 2011, primarily due to inadequate wastewater treatment in nearby areas[31]. These findings highlight the need to combat nutrient pollution in order to conserve and restore the ecological balance of Asian inland water systems.

North America

HABs are prevalent in North American lakes, with CyanoHABs documented in inland waters across all 50 states in the United States[32]. Nutrient pollution from many sources, such as municipal wastewater

Table 1 | Typical bloom-forming phytoplankton in inland waters

Kingdom		Genus	Toxic	Nutrient limitation		Preferred environments		
				P	N	Stratification	Warm	High light
Cyanobacteria/blue-green algae	Non-N_2-fixing	Microcystis	√	√	√	√	√	–
		Oscillatoria	√	√	√	√	√	–
		Planktothrix	√	√	√	√	√	–
		Gomphosphaeria	–	√	√	√	√	–
		Woronichnia	√	√	√	√	√	–
	N_2-fixing	Raphidiopsis	√	√	–	√	√	–
		Aphanizomenon	√	√	–	√	√	√
		Nodularia	√	√	–	√	√	√
		Gloeotrichia	√	√	–	√	√	√
		Dolichospermum	√	√	–	√	√	√
Chrysophyta/golden algae	–	Chromulina	√	√	√	√	–	–
		Chrysochromulina	√	√	√	√	–	–
		Dinobryon	√	√	√	√	–	–
		Mallomonas	√	√	√	√	–	–
		Prymnesium	√	√	√	√	–	–
Green algae	–	Botryococcus	–	√	√	√	√	√
		Chlorococcus	–	√	√	√	√	√
		Sphaerocystis	–	√	√	√	√	√
		Spirogyra	–	√	√	√	√	√
		Nitella	–	√	√	–	–	√
Cryptophyta	–	Cryptomonas	–	√	√	√	–	√
		Rhodomonas	–	√	√	√	–	√
Diatoms	–	Cyclotella	–	√	√	√	–	–
		Coscinodiscus	–	√	√	√	–	–

Different bloom-forming algae species can exhibit variations in toxicity, growth rates, nutrient requirements and preferred environments[164–166]. Ticks indicate preference and dashes indicate a negative or neutral response.

discharge and runoff from agricultural and urban areas, is considerd the primary driver of HABs in North American lakes[11,33–35]. In 1972, binational restoration efforts between the United States and Canada led to about 50% reduction in the annual total phosphorus input to the western basin of Lake Erie from 1974 to the late 1980s[36] (Fig. 3a). Reductions in nutrient loads have led to decreases in HAB occurrence in some US inland waters since the late 1970s and early 1980s, especially in western Lake Erie[37]. However, these measures did not remain consistently effective over time and varied by location. For example, despite a reduction in phosphorus inputs, Lake Erie has seen a resurgence in HABs since the 1990s with toxic algal blooms occurring most years[38,39] (Fig. 3c). Lake Winnipeg, whose watershed drains 90% of Canada's agricultural land, also continues to experience extensive and prolonged HABs[40–42]. The increase in HAB frequency in these lakes is attributed to diffuse agricultural nutrient sources increasing nutrient loading in the lakes, which is further exacerbated by rising temperatures and climate extremes enhancing stratification and favouring higher algal growth rates[39,43]. Such temporal and spatial variations in the trends in HAB occurrences across North America indicate an influence of the complex interplay of human activities and climate change[1,44,45]. However, the modest rise in bloom frequency indicated by satellite observations[1] contrasts with in situ observations from 323 US water bodies that suggest that chlorophyll-*a* levels are decreasing in more lakes than they are increasing[44]. This discrepancy highlights that observational approaches could also influence the observed trends in HAB dynamics and their variability.

Europe

HABs in Europe pose risks to water quality and safety, biodiversity and recreational activities, although their frequency is comparatively lower than on other continents[46–49]. In Hungary, Lake Balaton, the largest lake in Central Europe, has experienced HABs since the late 1960s, driven primarily by nutrient pollution from agricultural activities across its watershed and urbanization along its shores[50,51]. Despite improvements in water quality due to mitigation measures and agricultural collapse resulting from political changes in the late 1980s[52], a very large algal bloom occurred in Lake Balaton in 2019[47] (Fig. 3b,d). This bloom was not explained by external nutrient loading but was instead primarily driven by increased stratification due to warming and enhanced internal phosphorus loading[47] (Fig. 3b).

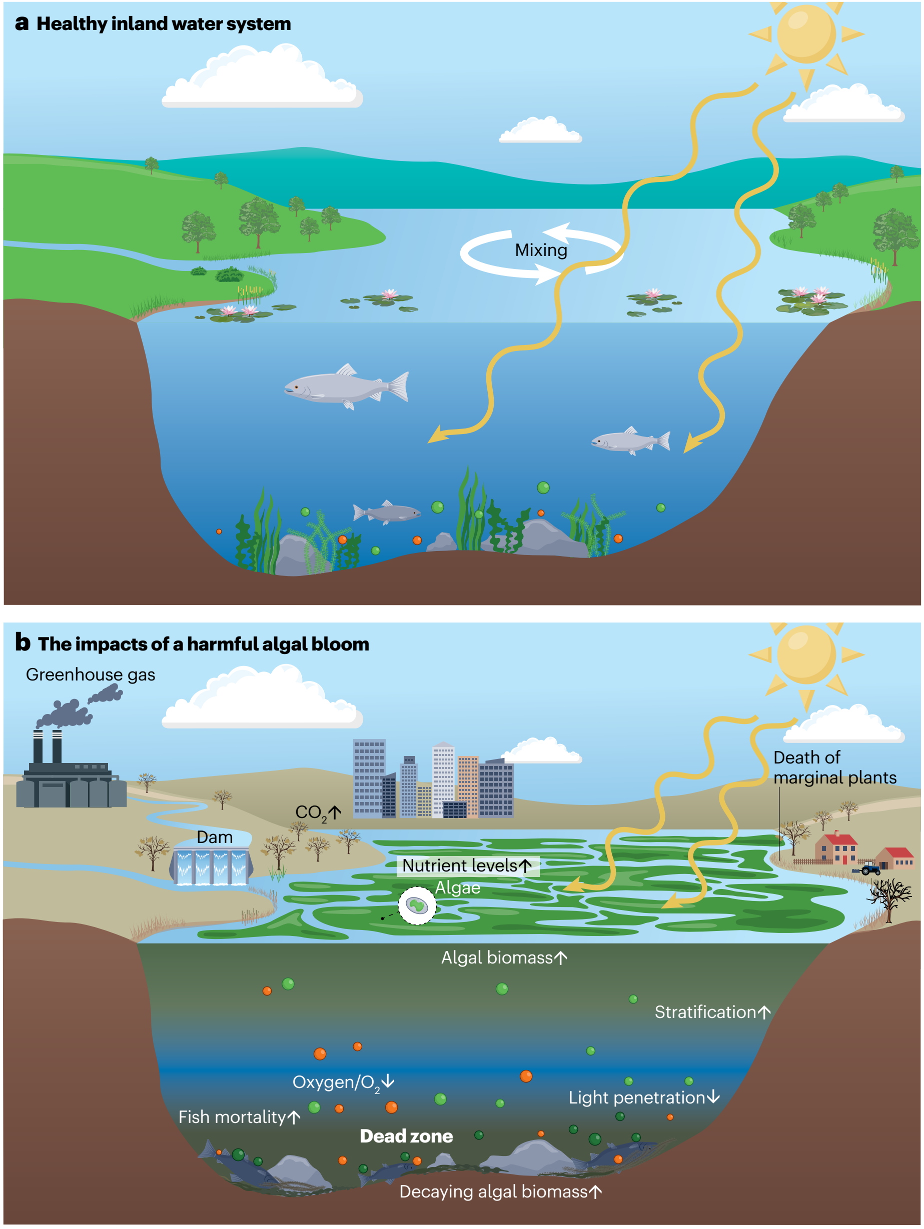


Fig. 1 | Summary of the impacts of harmful algal blooms on inland waters. a, A healthy inland water ecosystem, with good water visibility, benthic macroalgae, an oxygenated water column and fish. **b**, An inland water ecosystem affected by harmful algal blooms (HABs), with excess nutrients, proliferation of algal biomass, degraded water quality and poor visibility, limited benthic macroalgae, depleted dissolved oxygen concentrations, and fish mortality. HABs in freshwater ecosystems can cause severe ecological, societal and economic consequences.

Overall, while the incidence of HABs in European lakes has remained relatively stable since the 1970s owing to the implementation of actions to mitigate nutrient pollution[53,54], the resurgence of blooms in Lake Balaton and some lakes south of the Alps highlights that there are ongoing challenges in mitigating HABs, particularly in a warming climate[47,55].

Africa

High agricultural activity and untreated wastewater in Africa contribute to elevated nutrient levels and more frequent HAB occurrences in inland water systems[56–58]. Satellite data indicate a surge in bloom frequency across 21 African countries between the 2000s and the 2010s[1], which posed both ecological and public health risks[58,59]. HAB occurrences in Lake Victoria, Africa's largest Great Lake, are increasing in response to enhanced nutrient inputs from agriculture, deforestation and untreated sewage discharge, which has in turn led to mass fish mortality and disease outbreaks[60,61]. Similarly, Lake Naivasha in Kenya has experienced more HABs due to invasive species, excessive water extraction and vegetation loss[62]. The sharp decline in water levels has greatly reduced the large plant communities, primarily composed of papyrus, which serves as a natural filter for sediment and erosion materials in the watershed[63]. In South Africa, where drinking water scarcity is an issue, cyanobacterial blooms have occurred in 23 of the 50 largest reservoirs between 2002 and 2012, exacerbating the issues of poor water quality and drinking water availability[64]. Improved observational coverage and monitoring of HAB occurrences would help to mitigate and address issues surrounding water scarcity and security across the continent.

South America

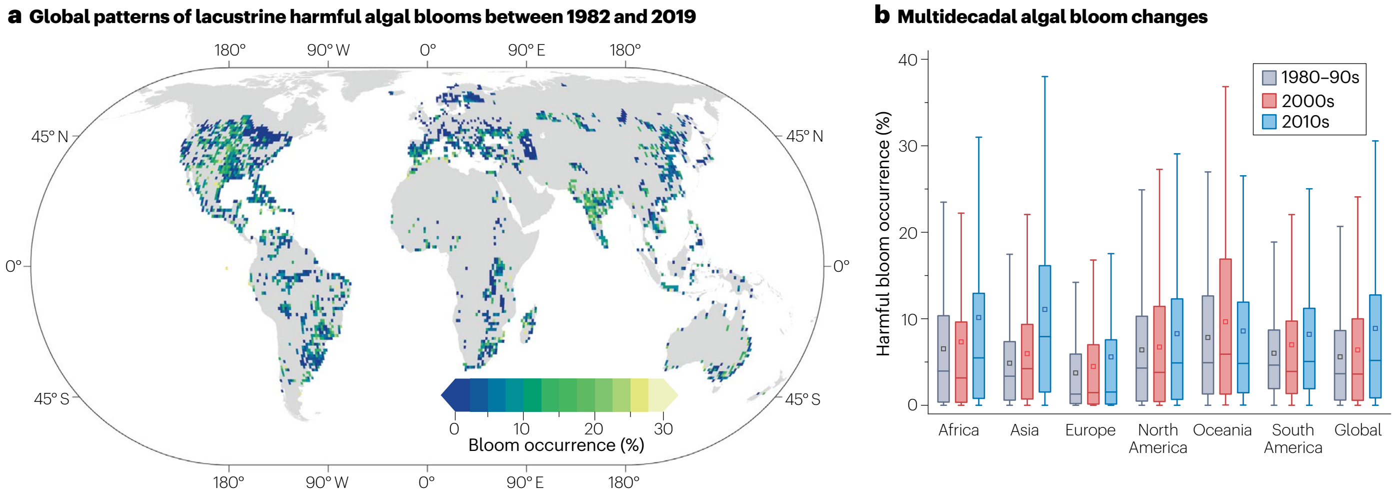
South America experiences the highest occurrence of HABs globally, with HABs affecting 14.3% of lakes with a surface area above 0.1 km^2 (ref. 1). Large-scale damming and water diversion projects, particularly in Brazil and Argentina, create favourable conditions for algal growth by reducing water flow, accumulating nutrients and enhancing stratification, as key drivers[65]. Contamination of these reservoirs can pose health risks, as many of them are vital water sources for drinking and agriculture[66–69]. In 2004, Brazil put legislation in place to regulate that microcystin levels in drinking water must not exceed 10 μg l^{-1} in samples taken over a period of more than 3 months[70]. However, HABs in South American lakes continued to increase during the 2010s[1,16], which was attributed to inadequate wastewater treatment and overuse of fertilizers[71,72].

Oceania

Despite Australia reporting the world's first documented toxic algal bloom, which occurred in Lake Alexandrina in 1878[73], Oceania experiences fewer inland HABs than other continents, and HAB frequency in Oceania has decreased overall since the 1970s[1]. That said, in New Zealand, HABs have occurred in lakes such as Ōtūwharekai, Wakatipu and Taupo, owing to increasing nutrient inputs from intensive agriculture and urban expansion[74].

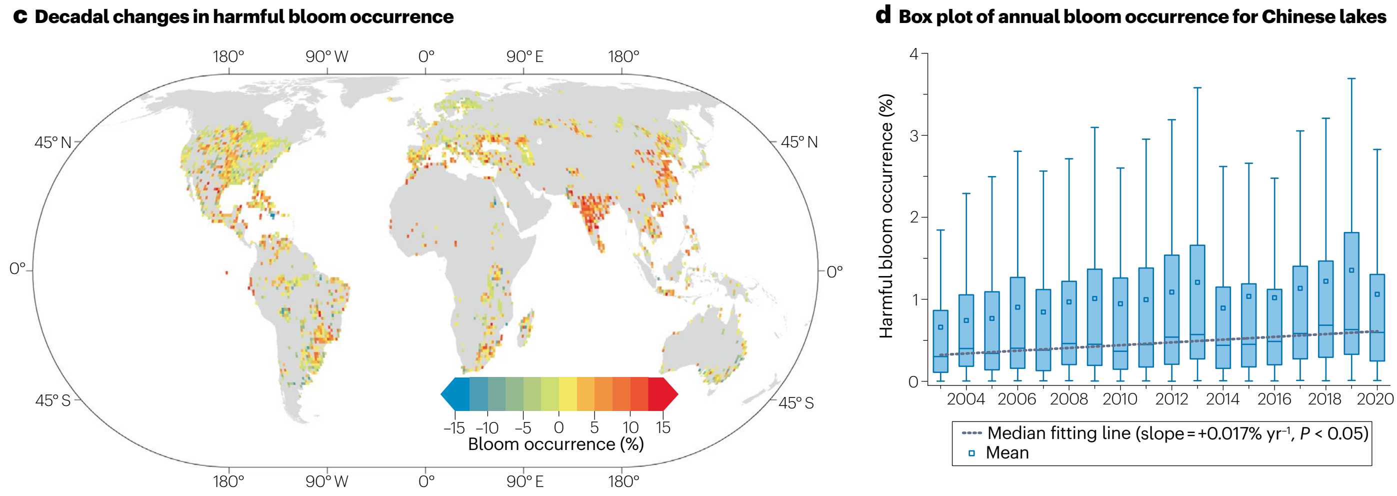
Limitations in spatiotemporal coverage

HAB hotspots have been reported across all the continents considered here (Supplementary Figs. 1 and 2). However, it is important to recognize the spatiotemporal limitations of prior investigations.



a Global patterns of lacustrine harmful algal blooms between 1982 and 2019

b Multidecadal algal bloom changes



c Decadal changes in harmful bloom occurrence

d Box plot of annual bloom occurrence for Chinese lakes

Fig. 2 | Global patterns and trends in harmful bloom occurrences in lakes. **a**, Global occurrence patterns of harmful lacustrine algal blooms between 1982 and 2019 aggregated into 1° × 1° grid cells and expressed as a percentage of total observational bloom number over the time period. **b**, Box plots of harmful algal bloom (HAB) occurrence (%) separated by continent and time period; the bottom and top of the boxes are the first and third quartiles, respectively, the bar in the middle shows the median, and the whiskers show the minimum and maximum values. **c**, Change in harmful bloom occurrence from the 1980–90s to the 2010s expressed as the percentage change in annual bloom frequency in each location. **d**, Annual HAB occurrence for large, bloom-affected lakes in China, expressed as a percentage of the total number of bloom-containing pixels over the total number of cloud-free MODIS pixels within a year. The data in panels **a**–**c** were extracted from Landsat images[1], and the data in panel **d** are from the Moderate-resolution Imaging Spectroradiometer (MODIS)[20]. Although most global studies show a general increase in HABs in recent decades, the trends vary by region and time period.

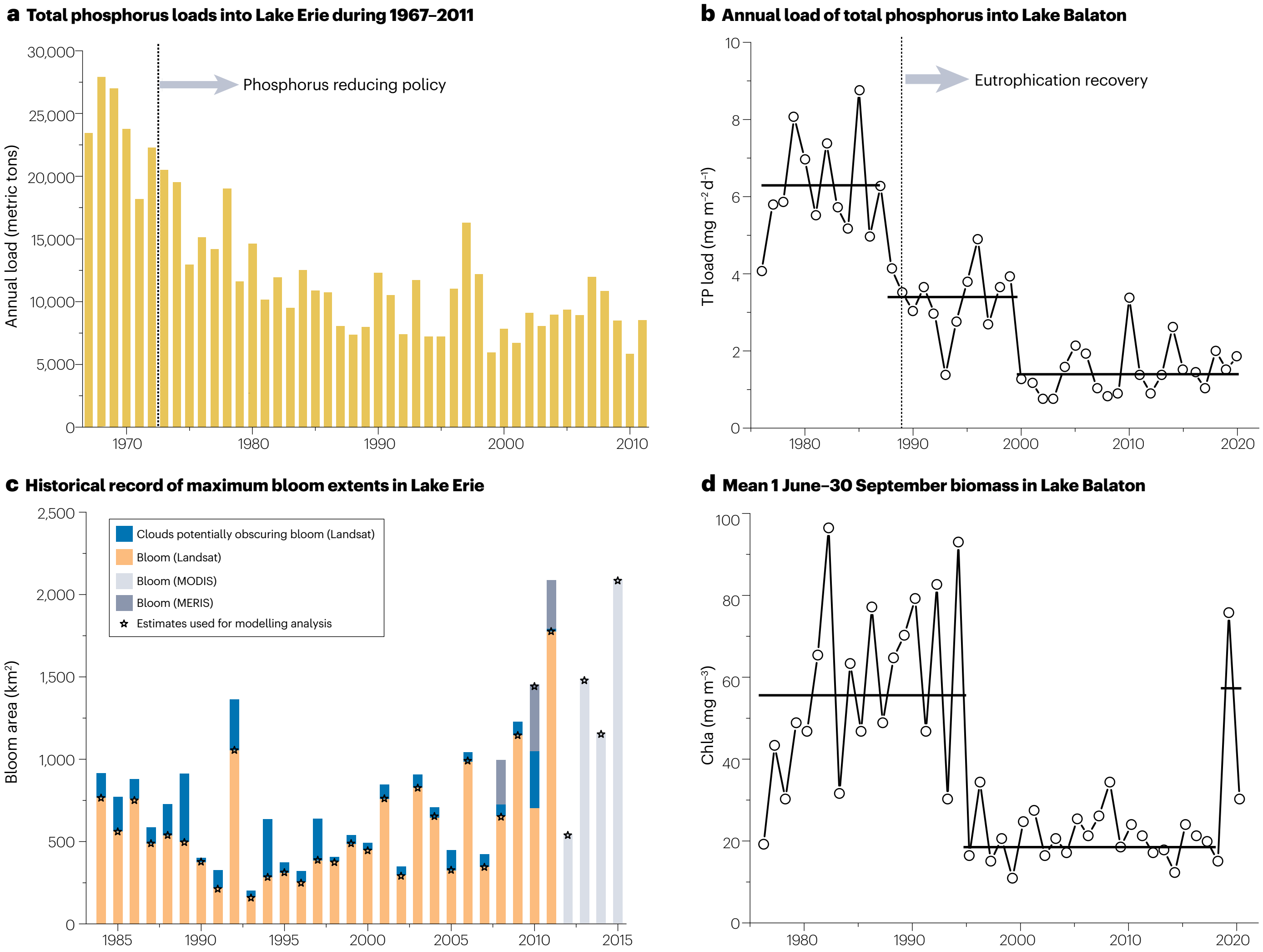


Fig. 3 | Changes in nutrient loads and algal biomass in Lake Erie and Lake Balaton. a, Annual total phosphorus loads (annual load, metric tonnes) delivered to Lake Erie from 1967 to 2011[95]. **b**, Daily total phosphorus load (TP load, mg m^{-2} d^{-1}) delivered to Lake Balaton from the 1970s to the 2010s[40]. **c**, Maximum summertime bloom extents in Lake Erie from 1984 to 2015 derived from various satellite products and model analysis estimates[167]. **d**, Mean summertime chlorophyll-*a* concentration (Chla, mg m^{-3}) in Lake Balaton from the 1970s to the 2010s[47]. The horizontal lines in **b** and **d** indicate mean values during periods of time representing different nutrient management regimes. Despite reductions in total phosphorus loads in both lakes, Lake Erie has experienced an increase in harmful algal bloom occurrence since the 1990s whereas Lake Balaton experienced an increase in 2019.

There is an imbalance in geographical coverage of HAB studies. Most studies have focused on lakes in high-income countries, with approximately 65% of the relevant literature being focused on just 20 inland lakes (Supplementary Fig. 2). Remote-sensing data have provided insights into HAB events occurring in over 20,000 lakes globally[1], indicating a clear need for in situ studies of HABs to be conducted widely. HAB occurrences are known to be prevalent in a number of African nations, and in several countries in Asia (including Indonesia, Pakistan and the Philippines) and South America (such as Chile and Colombia), despite there being limited research on HABs in these regions[1] (Fig. 4). The insufficient attention given to these areas can be attributed to various factors[6], such as economic constraints, the relatively minor socioeconomic impact of HABs in remote locations, and other contextual circumstances[75].

Short-term HAB dynamics need to be better characterized. Some bloom-forming phytoplankton species can migrate vertically through the water column to locate optimal growth conditions, according to temperature, light availability and nutrient availability[76,77]. Migratory behaviour leads to the surface features of colonies being highly variable in space and time, rendering them difficult to characterize[78]. For example, high-frequency (10-minute) remote-sensing observations have shown that the spatial extent of near-surface CyanoHABs in Lake Taihu, China, can vary by up to one order of magnitude within a single day[79]. Such rapid changes pose challenges for conventional field survey methods, which offer limited spatiotemporal coverage[80] while often having substantial labour and resource requirements. Satellite-based assessments of bloom extent are generally considered a more reliable approach[6]. However, satellite data also suffer from limitations in observation frequency and coverage. For example, Landsat images have a long revisiting period of 16 days and are often affected by cloud cover, which can limit the number of valid observations they can provide, particularly before the 2000s when fewer satellites and ground data receiving stations were available[81,82]. Even with higher-frequency satellite data, such as Moderate-resolution Imaging Spectroradiometer and Geostationary Ocean Color Imager, coarse spatial resolutions and/or limited spatial coverage can hinder their effectiveness in globally characterizing short-term HAB dynamics[83] (Supplementary Fig. 3).

There is a limited understanding of the vertical distributions of HABs[84]. Although surface scums provide a visible sign of HABs, their formation relies on calm waters and low wind speeds, and their absence does not necessarily indicate that a HAB is not present[78]. Most field measurements and satellite observations focus on surface water quality with limited monitoring of conditions beneath the surface, which can lead to the misconception that a lake is free of HABs[85]. The vertical distribution of algae is a function of the density of the cells, their gas vesicles, and the gas bubbles formed within colonies, and can be further regulated by the ambient environment, including temperature, light, wind and hydrodynamics[86–89]. Exploring the complex vertical distribution and dynamics of HABs in subsurface layers of lakes can provide valuable insights into the process of HAB formation and dissipation[90].

The study of HABs is geographically imbalanced and methodologically challenged by various factors, including the need for more in situ studies in underrepresented regions, the difficulties of characterizing short-term dynamics, and the limited understanding of vertical distributions. Addressing these gaps is crucial for a comprehensive understanding of HABs and their global impact.

Drivers of HABs

The drivers that influence the growth, motility and collapse of HABs in lakes can broadly be categorized into three groups: nutrients, climate

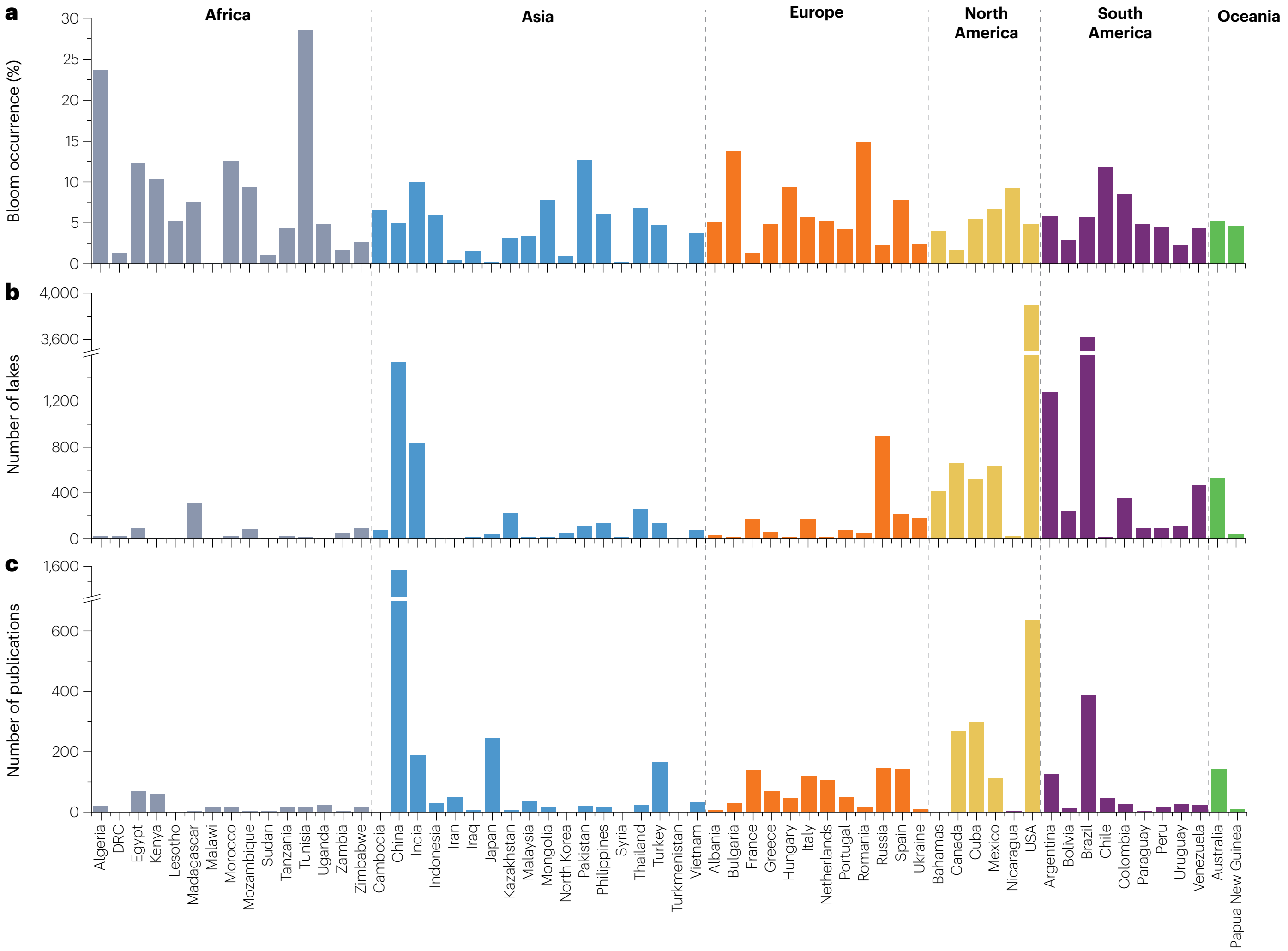


Fig. 4 | Limitations in the spatiotemporal data coverage of regional harmful algal bloom occurrences. a, Mean occurrence of harmful algal blooms (HABs) in lakes between 1982 and 2019 separated by region, where harmful bloom occurrence is defined as the percentage of the total observations during which blooms were detected over the time period[1]. **b**, Number of bloom-affected lakes detected between 1982 and 2019[1]. **c**, Number of research articles on HABs from each region published between 1907 and 2022 (see Supplementary Methods). Lakes in some low-income countries, which have received less attention in HABs research, may face a higher risk of more severe HAB outbreaks.

change or climate extremes, and hydrodynamics (Fig. 5). In this section, we discuss the causes and feedback mechanisms associated with these drivers, and the implications for future trends in HABs.

Nutrient enrichment

A fundamental driver of HABs is enhanced nutrient availability. Phosphorus and nitrogen are crucial nutrients for algal growth, having a pivotal role in various biological processes such as cell division, chlorophyll synthesis, and biomass production and accumulation[76]. Phosphorus constitutes an integral part of all nucleotide structures found within algae cells, and the role of adenosine triphosphate is intricately connected to energy conversion processes in organisms[91]. Nitrogen, a fundamental component of chlorophyll and proteins, is essential for photosynthesis[92]. Increases in global fertilizer use since the 1960s has resulted in widespread nutrient pollution that has, in turn, led to HABs becoming a pervasive and worldwide environmental concern[93]. Eutrophication and the proliferation of HABs are further exacerbated by increases in nutrient inputs to inland waters from industrial pollution, aquaculture and animal husbandry activities[94,95].

The traditional view that phosphorus has a crucial role in promoting cyanobacterial blooms is grounded in the results of a 37-year fertilization experiment carried out in the Ontario Experimental Lake District in Canada[96]. However, the nitrogen-fixing algal species used in the experiment, which included *Anabaena* and *Anophyllum*, are able to assimilate nitrogen from the atmosphere. Thus, phosphorus rather than nitrogen was the nutrient primarily limiting growth and production of algal biomass in the experiment[96]. For non-nitrogen-fixing species, the control of nitrogen availability remains crucial in reducing the incidence of HABs[97]. Indeed, solely reducing phosphorus concentrations in waters has shown only temporary effects in many lakes, such as Lake Erie, USA, where non-nitrogen-fixing cyanobacterial species such as *Microcystis* have become dominant and persistent[98]. Hence, it is now widely acknowledged that inland water HABs are influenced by both nitrogen and phosphorus[98]. In general, the relationship between algal biomass and nitrogen, phosphorus or their ratio is highly variable among different algal species and ecosystems, and even between different seasons[99].

Climate change and weather extremes

Climate change and weather extremes have strongly influenced the occurrence of HABs in inland lakes[100], with increasing evidence that global warming is contributing to the rise of HABs in inland waters worldwide[101]. Reductions in fertilizer use in some developed nations[102] have led to warming and extreme climatic events becoming the primary factor when predicting and assessing the risk of HAB formation[103]. Climate variability is particularly influential in highly eutrophic systems, where nutrient levels are sufficiently high that their availability is no longer the primary factor limiting HAB occurrence[104]. For example, despite the efforts of government policies to reduce point-source and non-point-source pollution across their watersheds, China's Taihu and Chaohu lakes continue to receive nutrient loads that make them prone to algal blooms due to high levels of urbanization and intensive agriculture in the surrounding areas[25,105]. As nutrient levels continue to be sufficient to support HAB

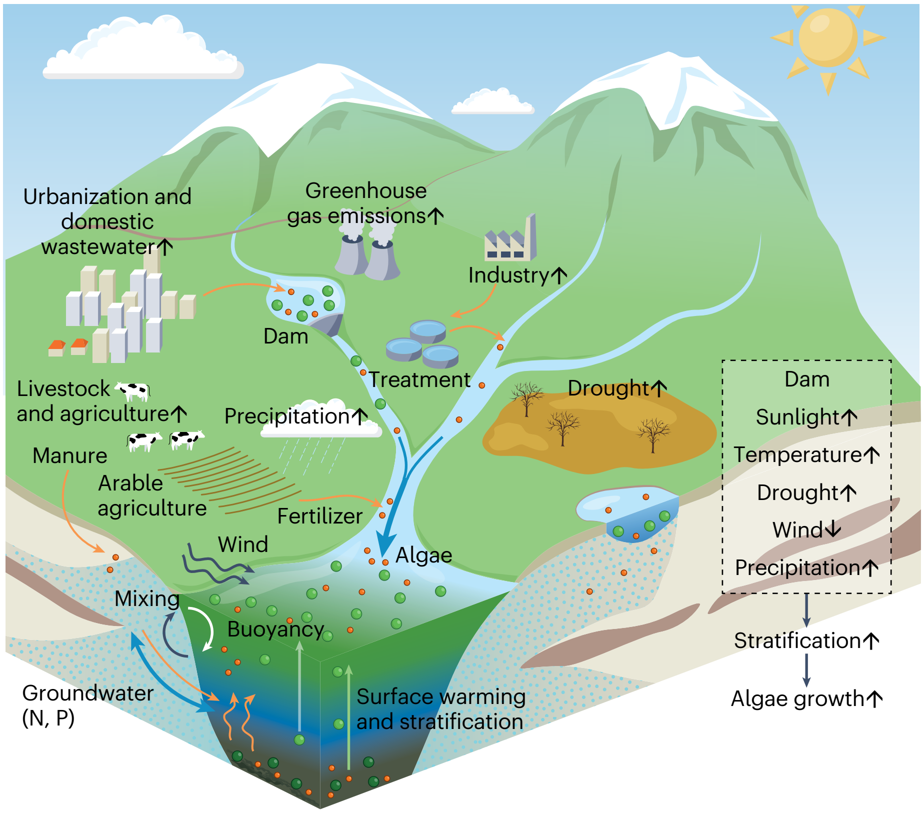


Fig. 5 | Factors influencing the formation of harmful algal blooms. Climate-change-induced warming and precipitation changes, and human-activity-induced nutrient pollution and lake hydrodynamics, influence the formation of harmful algal blooms (HABs) and resulting ecosystem impacts. Black upward arrows next to factor names indicate factors that promote HAB formation, and black downward arrows indicate factors that inhibit HAB formation. The orange arrows indicate the nutrient transport pathways. The effects of nutrients, hydrodynamics and climate change on HABs are complex and interrelated.

formation, the continued increase in the severity of cyanobacterial blooms in these lakes is thought to be driven by warming and extreme climate conditions[103].

Temperature directly affects metabolic, photosynthetic and growth rates of algae[106], such that algal growth and reproduction can be stimulated by warmer temperatures. The maximum growth rate of HAB-forming cyanobacteria typically occurs at temperatures above 25 °C, exceeding the optimal growth temperatures of non-HAB-forming species such as diatoms and dinoflagellates[107]. Laboratory studies indicate that the growth rate of cyanobacteria increases more rapidly than that of eukaryotic primary producers under the same rate of warming[108]. Additionally, cyanobacteria are more adaptable to elevated temperatures than other algae species, which contributes to their increased prevalence in HABs under global warming[109]. Stratification can also favour buoyant cyanobacterial species as it allows them to accumulate in the well-lit and warm surface waters to form blooms[110]. Warming also extends the growing season for algae in inland waters, as the onset of seasonal stratification occurs earlier in the spring and the breakdown of stratification occurs later in the autumn[8]. Overall, although the stimulative effects of warming on HABs have been identified globally, the synergistic interaction between warming and nutrient enrichment is complex[111]. Consequently, it remains unclear whether climate warming or nutrient enrichment is the dominant factor driving the global increase in HABs in inland waters[112].

Daily and weekly changes in meteorological conditions also affect the outbreak of HABs. High winds can induce vertical mixing and drive sediment resuspension and nutrient upwelling, potentially leading to elevated nutrient concentrations and enhanced algal growth[113]. Precipitation influences water temperature, stratification and flow, in addition to influencing nutrient transport in the surrounding catchment and nutrient loading to the water body, all of which can influence HAB dynamics[114]. Events such as tropical cyclones, thunderstorms and droughts can also stimulate HABs by altering nutrient transport, transformation and accumulation[100,115]. For example, in Lake Taihu, the area of algal blooms expanded from less than 200 km^2 to around 400 km^2 within 4–5 days after tropical cyclones passed over the lake, owing to these events driving enhanced sediment resuspension and nutrient release[116]. The optimal conditions for cyanobacterial growth seem to occur when heavy rainfall is succeeded by drought[76], owing to intense rainfall increasing nutrient runoff and drought extending the residence time of nutrient-rich waters. This sequence of events is becoming more common globally in the context of global warming[117].

Hydrodynamics

Water residence time, lake morphology and artificial dams all affect the hydrodynamics of inland waters and influence the growth of phytoplankton[118,119]. Lakes with long water residence times and limited hydrological connectivity favour enhanced nutrient trapping and promotion of algal growth and bloom formation[120] (Table 1). Lake morphology, including size, depth and shoreline complexity, also influences the growth and spread of algae by governing the internal biogeochemical cycling dynamics within the lake ecosystem[118,121]. For example, a global statistical analysis showed that shallower lakes (mixing depth > maximum depth) tend to be more susceptible to eutrophication, exhibiting nitrogen limitation in most cases (66.2%). In contrast, phosphorus limitation primarily prevails (94.4%) in most lakes, particularly those characterized by greater depths, where phosphorus is less readily released into the water column from the suspension of buried bottom sediments[121]. The relationship between mixing depth and water depth, as well as the extent of sediment–water interface, can also influence nutrient availability and the trophic status of lakes by affecting in-lake nutrient cycling processes[26,122]. For example, Lake Taihu in China, a shallow system, nutrient loss from the water column and sediment burial are hindered by frequent wind-induced sediment resuspension[26].

The global landscape is punctuated with a multitude of reservoirs, where human interventions in water management have emerged as the predominant driver of fluctuations in global surface water storage[123]. Riverine reservoirs formed by dam construction increase the potential for HAB formation, owing to associated changes in water flow and stratification patterns resulting from the manipulation of water levels through dam regulation[124]. For example, changes in hydrodynamic regime since the construction of the Three Gorges Dam in China have led to various types of HABs occurring annually since the first incidence of a toxic cyanobacterial bloom in a tributary of the reservoir in 2008[125,126]. Conversely, the operation of reservoirs can be optimized to potentially mitigate against HABs in downstream water bodies by increasing their flushing rates[127].

The formation and persistence of HABs in lakes are driven by a complex interplay of nutrient enrichment, climate change and hydrodynamic factors. Understanding these drivers and their interactions is crucial for predicting future trends in HABs and developing effective management strategies to mitigate their impacts on freshwater ecosystems and human health.

Future trends in HABs

Most projections of future trends in HAB occurrences indicate overall increases under various emission scenarios due to the intensification of climate change and human activities[128], but these projections carry considerable uncertainties. An integration of climate change projections with hydrological and water quality network models predicted that the mean number of HAB occurrences in US lakes would increase from 7 days in 2024 to 18–39 days by 2090[129]. Statistical models based on historical observations predict an increase of 111% in phytoplankton on average across 29 lakes in Europe and North America by the mid-twenty-first century[130].

The projected widespread increase in HABs is based on the current understanding of natural and anthropogenic drivers of HAB formation. Climate-change-related temperature increases are likely to lead to an increase in HAB occurrences due to the stimulating effects on bloom formation through raising algal growth rates, lengthening the growing season and enhancing water stratification. Rising atmospheric levels of carbon dioxide will also provide favourable conditions for photosynthesis and CyanoHAB growth[131]. Cyanobacterial blooms can form buoyant surface colonies that develop into scums that block light from penetrating the water column and hinder photosynthesis and growth of more desirable eukaryotic algal populations[132]. This, in turn, reinforces the dominance of CyanoHABs[132].

Future climate change is expected to bring more extreme events of both heavy rainfall and drought[133]. Extreme drought conditions prolong the residence time of inland waters, which promotes the occurrence of HABs[76]. However, changes in precipitation patterns could either exacerbate or inhibit HABs depending on the location, the morphological characteristics of the water body, or the growth stage of the bloom itself[114,134]. In the short term, heavy rainfall can temporarily disrupt the proliferation of cyanobacteria through enhanced vertical mixing and flushing[135]. However, intense rainfall can enhance nutrient runoff, leading to an increase in nutrients downstream[76]. Future changes in land use and the associated changes in catchment nutrient flow will affect nutrient loading of inland water and HAB risk. This nutrient loading could be particularly pronounced in low-income countries with a heavy reliance on use of agricultural fertilizers to enhance food security[1].

There is substantial uncertainty in current future predictions. Process-based mechanistic methods that apply rigorous mathematical equations to characterize how physiological and environmental factors affect phytoplankton growth are highly sophisticated but still have shortcomings in several areas[136,137]. For instance, quantification of how different phytoplankton species will respond to climate changes remains limited[138]. Laboratory-based insights into the response of phytoplankton growth to various environmental conditions do not always align with real field responses or conditions, including interlake variations in environmental factors such as geography and hydrology[100,139]. Additionally, numerical simulations and future projections will need to accurately represent changes in climate and human activities, such as land use and dam construction, to reduce uncertainties in predicted internal and external lake nutrient loading and cycling dynamics[100,140].

Although projections generally indicate an increase in HAB occurrences due to climate change and human activities, substantial uncertainties remain. Addressing these uncertainties through improved understanding of environmental interactions and enhanced modelling techniques is crucial for developing effective HAB management strategies in the future.

Management

Several government bodies have implemented a range of measures to mitigate the incidence of HABs and the ecological and socioeconomic risks that they pose. The regulation of nutrient levels is often the central focus in controlling and managing HABs. Initiatives to reduce nutrient pollution in inland waters were implemented in the United States, Canada and other countries and regions during the 1970s and 1980s[39]. Lake Biwa in Japan provides an example of successful algal bloom mitigation through effective conservation measures such as maintaining good water quality, improving soil recharge capacity, and preserving natural environments and scenic landscapes[141]. These efforts have substantially reduced eutrophication rates, resulting in clearer lake waters that have transitioned to being dominated by macrophytes since 1994[142]. Conversely, a 2012 National Lake Assessment by the US Environmental Protection Agency found that nitrogen and phosphorus concentrations were elevated in approximately 35% and 40% of lakes, respectively[143], indicating the ongoing need to control and reduce nutrient inputs. In 2011, the US government launched a 25-year initiative called Project Clean Lake that is dedicated to mitigating sewer overflow discharges into the Great Lakes[144]. The project aims to reduce annual discharges of raw sewage into Lake Erie by 4.0 billion gallons by 2036, which is expected to also alleviate HAB issues. This extensive endeavour includes the construction of substantial storage tunnels, improvements and expansions to wastewater treatment plants, and the integration of green infrastructure such as stormwater control measures[145].

Despite successful control of nutrient levels, many lakes have experienced a resurgence of HABs since the 1990s that suggests that it is not always possible to mitigate against HABs through nutrient control alone[39]. In these instances, nutrient loading can be sustained by legacy sources, including nutrients held in catchment soils and lake sediments[146,147]. Thus, effective strategies for nutrient reduction also need to consider upstream management of soil erosion and ways to mitigate nutrient transfer between sediment and the overlying lake water column. Indeed, some nutrient management strategies have incorporated approaches such as sediment removal and, as in Lake Taihu, algal biomass harvesting[26]. However, such efforts require substantial investment, and large-scale implementation is challenging.

Another challenge is that nutrient level thresholds for HAB formation vary greatly between different water bodies and between different seasons and times[99]. Therefore, determining target nutrient thresholds to control HAB occurrences often necessitates individual lake-specific research. For example, to effectively control phytoplankton biomass within acceptable ranges in Lake Taihu, total nitrogen and total phosphorus concentrations should not exceed 0.80 mg l^{-1} and 0.05 mg l^{-1}, respectively[148]. In contrast, the water quality target of total nitrogen concentration for the Lake Winnipeg north basin is 0.70 mg l^{-1} (ref. 149). Moving forward, nutrient thresholds such as these should also be adjusted to take account of the direct and indirect effects of climate change on algal growth and HAB occurrence.

Additional management approaches, beyond nutrient control, can also be used to help to mitigate against HABs. Manipulating the hydrological structure of water bodies can act as a preventive measure against excessive algal growth, as altering the flow rate and water depth can disrupt the ecological niche of harmful algae[120,150]. However, the high cost associated with these methods reduces the feasibility of their widespread implementation. Introducing or increasing the abundance of natural predators, particularly herbivores, can be effective in limiting algal growth[76]. For instance, experiments in small ponds in western Victoria, Australia, demonstrated that the introduction of zooplankton and carp predation effectively consumed algae, resulting in significantly lower algal numbers and biomass[151].

Nutrient control remains a primary strategy for HAB mitigation, but its effectiveness can be limited by legacy nutrients and varying thresholds across water bodies. A comprehensive approach incorporating diverse management techniques, including hydrological manipulation and biological control, is crucial for effective long-term HAB management, despite implementation challenges.

Summary and future perspectives

There is a heightened awareness of the widespread occurrence of HABs and the risks that they pose to human health and aquatic ecosystems[152]. Technological and methodological advances have had a pivotal role in enhancing understanding the distribution, toxicological and physiological characteristics of a diverse range of HAB species[153]. Agricultural expansion and intensification, urbanization and climate change are just some of the factors enhancing the prevalence and severity of HABs. Increases in HABs have, in turn, exacerbated water quality and water scarcity issues[13]. Controlling nutrient inputs to inland waters has contributed to HAB mitigation in some regions. However, in many regions, legacy nutrient pollution and warming have fuelled a resurgence in HABs despite successful reductions in nutrient loading[38]. Given that factors governing HAB formation and potential mitigation vary between individual water bodies, attaining a holistic understanding of HAB dynamics to enhance HAB prediction accuracy and mitigation efficacy is challenging[154]. As such, there remains a pressing need to develop integrated monitoring networks, establish comprehensive data-sharing platforms and leverage multisource data to overcome limitations in spatiotemporal coverage, enhance predictive capabilities and improve understanding of future trends in HABs.

Constructing integrated monitoring networks that combine in situ, aerial and satellite monitoring can facilitate large-scale and short-to-long-term observations of HAB occurrences and dynamics. A successful example is in Lake Erie, where the US National Oceanic and Atmospheric

Administration and its partners use satellites, buoys and genetic analysis of algal samples to comprehensively track HABs[155]. Advanced remote-sensing platforms with high-resolution hyperspectral sensors can fill gaps left by in situ HAB monitoring. These tools can identify specific algal species within blooms, enhancing our understanding of HAB impacts and toxicity. For example, in Montana's Upper Clark Fork River, researchers used a drone-mounted hyperspectral camera to capture detailed images of algal blooms, revealing their composition and spatial distribution with unprecedented clarity[6,156]. Integrating satellites, drones and in situ monitoring stations enables a comprehensive analysis of HAB dynamics by combining large-scale frequent observations from satellites, high-resolution targeted monitoring from drones, and detailed water quality data from in situ stations[157]. This integrated approach improves understanding of bloom initiation, growth, spatial distribution, and decline[158]. However, field surveys and laboratory analysis are essential for accurately determining algal biomass, composition and HAB toxicity. These observations provide ground-truth data to calibrate and validate remote-sensing algorithms, ensuring accurate satellite and drone data[159]. They also offer detailed insights into species composition and toxin levels, enhancing overall HAB monitoring precision.

The frequency of HAB events in a given location is relatively[1] low, meaning that there are limited data to advance understanding of HAB formation in that system. Establishing wider data-sharing mechanisms and promoting interdisciplinary research on HABs could help to shed light on the complex responses of HABs to environmental factors and nutrient dynamics. Achieving these goals requires standardizing monitoring protocols, creating centralized data repositories, and fostering collaboration among disciplines such as microbiology, phycology, ecology, limnology, climatology and water management. By integrating diverse expertise and data sources, researchers can achieve a more comprehensive understanding of HAB dynamics, leading to improved predictive models, effective management strategies and informed policy decisions[160]. Global and regional data-sharing systems collating HAB data provided by researchers, monitoring agencies, stakeholders, and the general public, through community reporting programmes[161,162], could help to develop a HAB database covering a diverse range of geographical locations. Sharing multiple types of datasets could also help promote collaboration among researchers from various disciplines. Notable examples of such interdisciplinary initiatives are the European Multi-Lake Survey (EMLS)[108] and the Global Lake Ecological Observatory Network (GLEON). The EMLS, involving scientists from 26 countries, successfully analysed and standardized data from 369 lakes across Europe, yielding valuable insights into how climate change affects the frequency of cyanobacterial blooms[108].

The future of research on HAB dynamics relies on integrating diverse data sources and advanced analytical methodologies. Using data resources from integrated monitoring networks, globally shared datasets and historical climate records holds great potential for elucidating the role of nutrient enrichment and climate variability in promoting bloom formation, understanding HAB formation processes and analysing HAB dynamics. Exploring these large datasets in depth will provide more nuanced and holistic insights into the factors influencing algal behaviour across a diverse range of natural ecosystems. The application of advanced methodologies, such as machine learning (for example time series data analysis, deep learning and ensemble learning), to these datasets could potentially reveal intricate and nonlinear relationships that govern responses of algal growth to environmental factors[154,163]. Through interdisciplinary collaboration among fields such as microbiology, ecology, environmental science and climate science, insights into a wide range of physiological and ecological processes of algae could be achieved, including their growth and nutrient uptake dynamics, interactions with other organisms and responses to environmental changes. Projects should aim to better understand genetic and molecular mechanisms, ecosystem interactions, climate impacts, nutrient dynamics and toxin production, and to develop predictive models that can address the complexities of algal blooms comprehensively. The subsequent advances should aim to enhance our understanding of HABs by focusing on detailed spatiotemporal dynamics, multifactorial environmental drivers, species-specific behaviours, climate change impacts, early warning system development and broader ecological consequences. By filling these knowledge gaps, researchers can refine predictive models to better forecast HAB occurrences globally and implement effective management strategies.

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Author contributions

L.F. and Y.W. researched data and wrote the first draft for the article. X.H., B.Q., T. K., F.Q., N.C., H.W.P. and C.Z. reviewed and/or edited the manuscript before submission.

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The authors declare no competing interests.

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